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THE LENGTH OF THE LIFE CYCLE OF A CLIMBING BAMBOO. A STRIKING CASE OF SEXUAL PERIODICITY IN CHUSQUEA ABIETIFOLIA GRISEB.*

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Certain plants are known to live vegetatively for many years, then flower and die. The most frequently cited example of this phenomenon is that of the century plant, *Agave americana*, which lives for a period of years without flowering, then sends up a tall, prominent inflorescence, and finally, after the maturing of the seeds, dies. This sexual periodicity is also characteristic of certain bamboos which blossom only after a cycle of years and then all simultaneously throughout an extensive region. The bamboos in the South Brazilian provinces of Santa Catharina and Rio Grande do Sul are said to blossom at intervals of about thirteen years, and *Bambusa arundinacea* on the west coast of Cisgangetic India blossoms at intervals of about thirty-two years (1). The complete and simultaneous dying off of the bamboos may in some communities prove disastrous by the wiping out of the chief available source of building material through the transformation of luxuriant bamboo forests into barren areas; or, it may prove of great economic value as a source of grain, especially when it comes, as it is said to (2), in times of drought and consequent famine.

The length of the interval of years varies greatly in different bamboos. Bean (3) reports that "*Bambusa tesselata* has been in cultivation for probably over sixty years, yet I have seen no record of its having flowered anywhere." In striking contrast with this is the case of *Arundinaria falcata* var. *glomerata* which flowers almost every year on a certain number of culms. The latter is a case of partial or sporadic flowering as contrasted with the complete and simultaneous flowering which is the rule among bamboos. Intermediate types also exist. Bean (3) mentions the case of *Arundinaria Simoni* which flowered on odd culms in the bamboo garden at Kew for several years. He says, "excepting that the flowering culms died, the plants were in no way affected. . . . They continued to flower in this way every year up to 1903, by which time we had almost come to regard *A. Simoni* as a perennial. In that year, however, the plants flowered on every culm, and, after producing an abundance of seed, died. After that

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not a single trace of leaf growth was ever visible and the plants were ultimately uprooted."

This peculiar periodicity in the life of bamboos was strikingly brought to my attention during a recent stay in Jamaica. On my first walk along the trail which runs from Cinchona to Morce's Gap in the Blue Mountains, my attention was called, by Dr. Duncan S. Johnson, to the many dead patches of the climbing bamboo, *Chusquea abietifolia*. Dr. Johnson re-

FIG. 1. An entanglement of dead *Chusquea abietifolia*.

marked that on three previous visits to Cinchona he had always found the Chusquea in full foliage, forming large entanglements which, like the tree ferns, stood out as a prominent feature of the tropical vegetation. The Chusquea was still there, interwoven into mats beside the mountain path or hanging in festoons above the trail, but the color was no longer green, for every plant seen on that first walk was dead. It was immediately suspected that this climbing bamboo had, true to the habits of its tribe, died as a result of profuse flowering following a long period of sexual inactivity. It seemed, therefore, advisable to collect all obtainable data bearing upon the life history of this Chusquea. These data here published will bring up to date the story of the life of the Jamaican Chusquea which was begun by Sir Joseph Hooker and Sir Daniel Morris thirty-three years ago. The present observations seem to fix the length of the life cycle.

The climbing bamboo, *Chusquea abietifolia*, is, in reality, a scrambler with no specialized climbing organs—although one's first encounter with the plant is likely to suggest the presence of vicious thorns, for the leaf midrib terminates in a very sharp, protruding point. The long, erect young shoots push upward among the surrounding plants and are held from slipping back by the subsequent development of whorls of leaves and lateral branches. The height attained seldom exceeds 30 feet, while the mats of interwoven stems are often 10 to 15 feet across. If high supports are lacking Chusquea succeeds very well in climbing over low shrubs. The maximum basal diameter of the old culms is hardly a quarter of an inch, in contrast to the 5- and 6-inch culms of the closely related *Bambos* (*Bambusa*) *vulgaris* of the Jamaican lowlands.

Chusquea abietifolia is little known outside of Jamaica. It has been reported (4) from only two other localities, both in the West Indies—

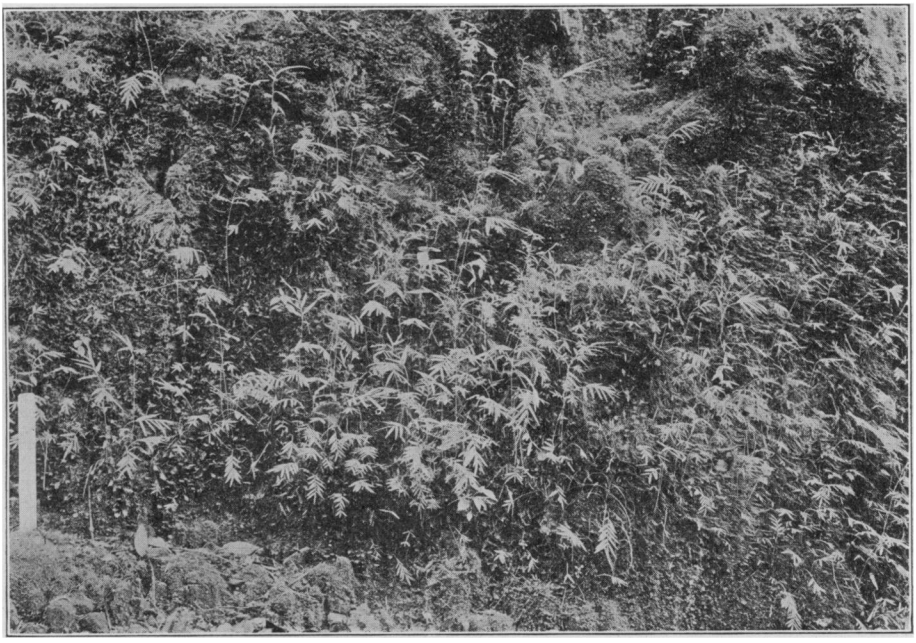

FIG. 2. Growing seedlings of *Chusquea abietifolia*.

Porto Rico (Monte Alegrillo) and Haiti (Monte Furcy). In Jamaica this rare bamboo is confined to the mountainous interior of the island. It does not occur much below 4,000 feet and is most abundant on the mountain ridges, being found on the very summit of Blue Mountain Peak, 7,360 feet above sea level.

The habitat of the plant is apparently not so definitely dependent on moisture as it is on altitude, although the lower limit of 4,000 feet is

possibly fixed by moisture requirements. Rainfall in the higher altitudes of these tropical mountains is always ample for vegetation, yet there is a pronounced difference in the soil moisture of exposed ridges and shaded ravines. Chusquea is found in both these regions; on the sunny, hot, dry spurs where vegetation is relatively sparse, and in the dark, cool, wet gulches where tree ferns and other moisture-loving plants abound. Chusquea is, however, most abundant under conditions intermediate between these two.

Published descriptions of this climbing bamboo are few and brief, that of Grisebach, in his *Flora of the British West Indies*, being among the earliest. A more complete systematic account by J. D. Hooker appears in the *Botanical Magazine* (Curtis) for 1885. The first definite reference to sexual periodicity in Chusquea appears in a short notice by Morris in the *Gardener's Chronicle* for 1886. He writes, "The flowering of this plant appears to take place, as in most Bambuseae, at long intervals."

The data pertaining to the life habits of *Chusquea abietifolia* published here were obtained from the following sources: first, from Wm. Harris, government botanist of Jamaica, to whom I am greatly indebted for many kindnesses during my stay on the island: second, from several published articles herein referred to, which were kindly brought to my attention by Assistant Director Arthur W. Hill, of the Royal Botanic Gardens at Kew: third, from the notes of Daniel Morris and J. H. Hart recorded in a copy of Grisebach in the library of Hope Gardens, Jamaica: fourth, from the natives living in the mountains, especially David Watt, whose long experience in collecting for Jamaican and visiting botanists has made him uncommonly familiar with the plants of the mountain forests: and lastly, from my own observations covering a period of six weeks and extending over a ten-mile stretch of the Blue Mountain Range.

During June, 1919, nearly all mature plants of *Chusquea abietifolia* in the Blue Mountains of Jamaica were dead. On the other hand, the ground in many places was covered with seedlings varying from an inch to 18 inches in length. Diligent search brought to light only a few patches of old, living plants. Still fewer specimens were found bearing fruit.

The first question which naturally arose was, when did this climbing bamboo last flower? I was informed that there had just ended a most profuse flowering of all plants in the mountains wherever seen, and that the time of flowering extended over more than a year. The question which next presented itself was, how long a time had elapsed between this and the last previous flowering? Definite information on this point was obtained from Mr. Harris, who writes, "Chusquea flowered generally in the Blue Mountain regions in 1885–6 and died down everywhere." This first recorded flowering period also extended over more than a year, as is evident from the note of Hart supplementing that of Morris. The latter states that Chusquea was first noticed in flower in the fall of 1884, and that in

1885 it flowered generally. Hart adds, "It flowered also in 1886 or rather continued flowering from 1885."

That the outcome of the recent flowering of Chusquea—the death of all mature plants and their replacement by innumerable seedlings—is identical with that following the last general flowering 33 years ago, is evident

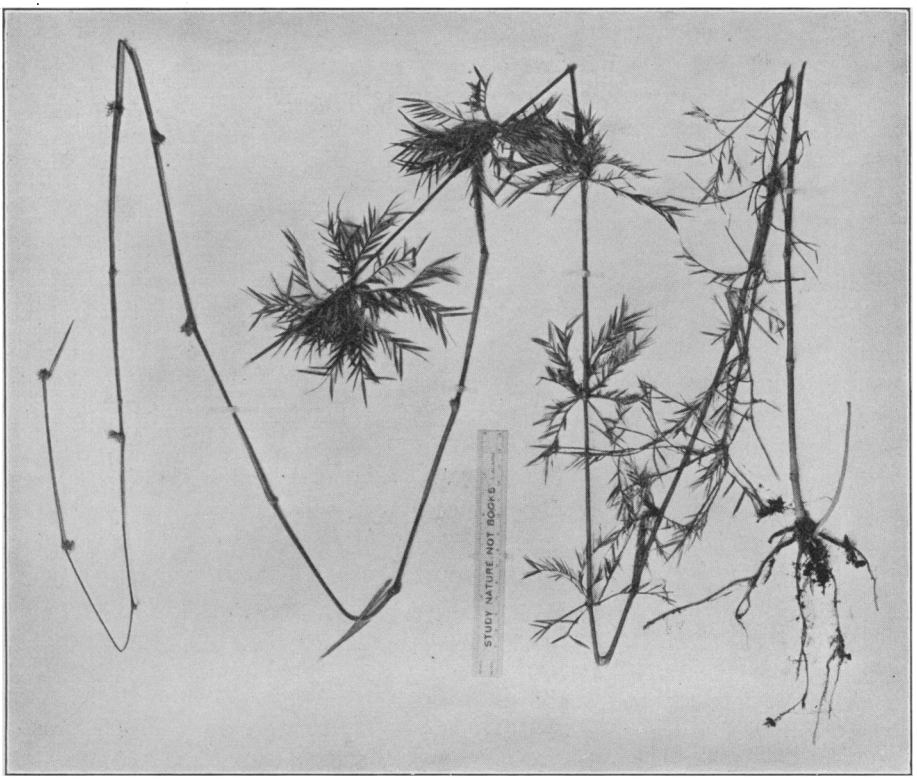

FIG. 3. An old basal culm of *Chusquea abietifolia* with a long, young, leafless shoot.

from the writings of the early observers. Morris (5) tells the story in this manner: The Chusquea "began to shed its leaves and to assume a dull, rusty color. . . . When the seed was set the stem began to die down, and apparently every plant in the island died, root and all. At the present time (1886) the ground in the forests where the Chusquea grew is covered with millions of seedlings, and in due time these will take the place of the former generation."

In 1884 some plants of Chusquea were sent in a Wardian case to the Royal Botanic Gardens at Kew. Hooker, referring to the Kew plants, wrote: "In December last (1884) they suddenly burst into flower causing me to fear that, after the manner of so many species of this most remarkable tribe of grasses to which they belong, they may not survive the flowering

period." The Kew plants died just as did the wild ones. It is worthy of special note that the Kew plants, after being transplanted to an entirely new and different environment, flowered simultaneously with the wild plants in Jamaica.

It is, therefore, immediately apparent that *Chusquea abietifolia* had just ended (in 1918) a life cycle of about thirty-three years during which time it had grown vegetatively only, until the last year when it flowered, disseminated its seeds, and died.

There are but three other species of climbing bamboo, all belonging to the genus Arthrostylidium. These also, like the Jamaican Chusquea, are found only in the West Indies. It is very probable that at least one of these other species goes through a cycle similar to that of *Chusquea abietifolia*. *Arthrostylidium sarmentosum* has been collected in flower only once (6).

Many days of tramping over the mountain trails near Cinchona revealed but a single green specimen of Chusquea, the only living plant among many hundreds of dead ones bordering the trail in the two-mile walk from Cinchona to Morce's Gap. Whether the presence of this sole living mature plant among so many dead ones is due to certain edaphic conditions which have delayed flowering and thus possibly produced a plant of altered life cycle, is uncertain. Its possibility will be discussed in detail later.

The ascent of Blue Mountain Peak showed a similar state of affairs to exist in that locality. The trail to the summit was lined with innumerable patches of dead bamboo. Several green plants were found but these few were not fresh and thriving in appearance, being apparently in a dying condition.

Some days later I learned of green plants growing on an exposed, rocky spur. Investigation first revealed short, fresh, green tufts of Chusquea, which proved to be young shoots from old rootstocks. This region had recently been burnt over. The charred stubble was still evident. The presence of green Chusquea here seemed easily explainable: the parent plants had been burnt to the ground before their life cycle was complete, and the living rootstocks had sent up new shoots which were continuing the growth of the plants and thus carrying on the vegetative portion of the life cycle beyond the normal limit. Opposed to this supposition is the statement of Hackel (7) that small plants from cuttings or layers of bamboos blossom at the same time as do the parents from which they were taken. It would be very interesting to determine experimentally just how such a catastrophe as the destruction of that part of the plants above ground shortly before their time of flowering would affect the normal life history of a plant like Chusquea.

Continuing along the spur above mentioned, I subsequently found a fair-sized area with numerous old but green and thriving plants. They were not in flower but were healthy, actively growing specimens, sending out an abundance of long, young shoots. Here was a prominent exception

to the general condition existing throughout the mountains. A noteworthy feature of the exception, however, was the fact that these healthy, green plants were all in a single and comparatively small area. The possibility of explaining their persistence by some external cause is, therefore, greater than would be the case had several distinct scattered groups been found.

The region in which these living plants are growing is one experiencing the extreme of mountain aridity above 4,000 feet. The ridge is hot and dry,

FIG. 4. Seedlings of *Chusquea abietifolia*.

and covered with vegetation characteristically xerophytic (*Pteris aquilina*, *Gleichenia Mathewsii*, *Agave americana*). Morce's Gap trail and Blue Mountain Peak, on the other hand, where Chusquea is, with few exceptions, to be found only as old, dead plants and young seedlings, are moist regions characterized by hygrophilous plants. Immediately below the dry area where the patch of living bamboos exists, there is a moist, shaded gulch where no living, mature Chusquea was found; for here, in an environment like that at Morce's Gap and on Blue Mountain Peak, the old bamboos are dead and seedlings are abundant. Here also flourishes a hygrophilous flora of tree ferns and succulent herbs. It seems, therefore, reasonable to conclude that the climbing bamboo has in this more arid region in some manner assumed an altered life cycle. The single green specimen, already referred to, found near Morce's Gap was growing on the hot and dry southwest slope of the mountain, a spot differing markedly from the nearby, shaded, semi-moist regions along the trail where Chusquea was represented by an abundance of dead plants and of living seedlings.

One rather welcomes an exception to the striking regularity in sexual periodicity of a species extending over a large territory. Indeed, one would expect not a single exception but many, brought about by different rates in seed germination, and in growth both of seedlings and mature plants due to differences in environmental factors such as moisture, light, temperature, and soil, which would ultimately give rise to plants whose time of flowering would precede or follow that of the majority, and which would thus, in time, produce many plants whose life cycles overlapped so that some out of the many could be found in flower in any year. It would be exceedingly interesting to attempt to bring about such a state artificially by deferring the sowing of the seed, and thus attempting to postpone the time of flowering or to shorten the life cycle. It would seem, however, that this experiment must have been many times performed by nature (*i.e.*, if the seed is capable of germinating after 1 or more years) so that we should be able to judge from the present condition of the wild plants of Chusquea whether the cycle can be altered in this way. Bean (3) is of the opinion that the simultaneous flowering of bamboos follows some general law. What this general law might be he does not suggest. Yet he does believe that under cultivation the system of simultaneous flowering of some of these species would appear to be breaking down, and he cites the case of *Arundinaria Falconeri* which flowered in England, in the vast majority of cases, in 1876, but the flowering of the generation at the time he wrote (1907) had already extended over five seasons. That a breaking down of simultaneous flowering in *Chusquea abietifolia* is taking place in the wild state is suggested by the exceptions that I have noted and by the fact that this climbing bamboo was detected in flower in 1911 and was also flowering freely at the base of Catherine's Peak, but not elsewhere, in November, 1912. In fact, Mr. Harris suggests, "It is just possible that individual plants of Chusquea may be found in flower in any year if careful search were made for them."

In spite of these several exceptions, it remains a striking fact that fully 98 percent of all plants of *Chusquea abietifolia* found in Jamaica in a region some ten miles in length, varying from 4,000 to 7,000 feet in altitude, and showing considerable diversities of light, temperature, and moisture, have flowered and died in a single brief period not exceeding two years, after a purely vegetative growth of more than thirty-one years.

This complete cycle of thirty-three years differs by only one year from that given by Brandis (8) for *Bambusa arundinacea* in India. It seems quite possible that the life cycles of these two genera are the same, for the exact time of flowering is not always readily determined. The general flowering of a species in one particular year may be heralded by a few forerunners the previous year and followed by that of laggards the next. Morris states that the last previous flowering of Chusquea in the Blue Mountains of Jamaica commenced in 1884, and Hart reports it as continuing until 1886. The exact time of the recent flowering is not definitely known.

David Watt is of the opinion that he first saw Chusquea in flower in the fall of 1917. I myself collected a few fruiting branches in the early summer of 1919. The climbing bamboo was, therefore, probably at the height of its flowering period in 1885 and in 1918, making the cycle one of thirty-three years.

I have referred to the possible effect of environment on change in time of flowering. Equally interesting, and possibly as difficult of solution, is

FIG. 5. Fruits of *Chusquea abietifolia*. Collector, William Harris.

the ultimate cause of the simultaneous flowering of nearly all plants in a certain locality. The obvious suggestion, often made in such cases, that this peculiarity is innate, does not, of course, solve the problem. It simply indicates that we must seek our explanation in causes operative before the initiation of the individual.

Attempts to associate the sexual periodicity of plants with seasonal or

other environmental changes may seem as far-fetched as to ascribe to climate or food the periodic appearance of the seventeen-year locust which has this year (1919) infested certain regions of our country. It is however, quite possible that the duration of the life cycle of plants exhibiting sexual periodicity is the direct result of certain known, present or past, stimuli. An apparently very clear example of such an association between season and periodicity is seen in the life cycle of annuals which flower and die at definite seasons of the year. But one can not always be certain that the most evident and seemingly controlling factor in such a case is the one at present active. A native annual in the temperate zone commonly rests in winter, germinates in the spring, fruits in summer, and dies in the fall. This sequence of events one is likely to attribute to the sequence of the seasons. Yet most annuals if grown in a greenhouse where seasonal changes are non-existent (except as to light) can, by sowing of seeds at the proper time, be made to fruit in any chosen month of the year without regard to seasonal conditions out of doors. Thus are the successive steps, from germination to death, in the life span of an annual grown in a greenhouse accurately maintained without evident relation to any external controlling factor. That is, the annual germinates, fruits, and dies in the same interval of time that it always has required, and does this in an environment quite different from the seasonally progressive one of its natural habitat. This behavior seems clearly to belie the validity of the assumption that the present seasonal round determines the duration of each phase of the developmental cycle, and thus of the cycle as a whole.

There are reported, however, examples of the flowering of plants being regularly brought on by such external factors as moisture. The following is such an example cited by Morris (5): "A prolonged drought in India is often accompanied by the flowering of the common bamboo, and on this account the natives associate the two phenomena in a manner which is emphasized by the fact that the bamboo grain during seasons of drought has provided them with the only available means of support." According to Ridley (cited by Schimper, 1) two species of Hopea and four species of Shorea blossom with great regularity every sixth year. These cycles are said to coincide with dry years. Morris (5) believes that the long intervals at which the flowering of Chusquea takes place probably depend "for their exact length upon the aspect of the prevailing seasons." Weather reports from Cinchona show, during the years preceding the recent flowering of Chusquea, no pronounced digression in temperature from the general average. The rainfall was unusually heavy for two years immediately preceding the flowering of Chusquea. It is hardly likely, though possible, that an over-abundance of rain should bring on a flowering period in Chusquea in Jamaica and drought be the cause of flowering of another bamboo in India.

Further proof against the theory that time of flowering is determined by

present seasonal factors is to be had from the behavior of the climbing bamboos sent to Kew. Morris (5) himself presents a bit of evidence against his own contention when he says, "Both the wild plants at Jamaica and the cultivated plants at Kew (although the latter were under such very different conditions) were in flower at the same time."

Should the life cycle of *Chusquea abietifolia* prove not to vary from the thirty-three years which it has been found to be—just as the cycle of *Bambusa arundinacea* has, from three successive observations (1804, 1836, 1868) been found to be exactly thirty-two years (1)—then it would seem hardly likely that the length of this term of years could be definitely ascribed to present climatic influences, unless there is some larger climatic round of years, such as that suggested by Brückner (9).

It is interesting to note, though of how much significance this may be is pure conjecture, that the climatic oscillation ascertained by Brückner (9) closely approaches in length of years the life cycle of Chusquea. There is, however, in addition to Brückner's 35-year alternation of wet and dry epochs, a supposed variation of rainfall in a cycle of eleven years, coincidently with the sunspot cycle (10). It is as yet by no means well established that climatic changes are periodic, and there is but little to support the idea that droughts occur rhythmically, especially with any great precision.

In considering the possible relationship between sexual periodicity in plants and climatic oscillations I have had in mind—as I assume others have had in their attempts to associate the two—only present climatic influences. That past rhythmical variations in rainfall or in temperature have, through the ages, fixed the life-cycle of Chusquea is quite possible. So striking is the association between the life of an annual and the seasons that it seems very probable indeed that the cycle of annuals is the direct result of seasonal influences, and that this cycle has, through many generations, become so firmly established as to be unalterable through the temporary elimination of seasons by transferring the annual to a greenhouse.

This problem can, however, and should, be attacked from other viewpoints than the purely ecological one. Other factors than such external stimuli as droughts and similar seasonal epochs may have been at work in establishing, or still are at work in maintaining, sexual periodicity in Chusquea. The problem may be of the same nature as that of puberty and senility in organisms. We know, for example, that certain organisms require a certain number of years in which to reach sexual maturity, and we know that certain organisms live about so long and never exceed a certain maximum. The present causes of such phenomena are not as yet seriously thought to be environmental in nature. That they may be somewhat influenced by environment is possible. Lack of food, for example, is said to hasten the attaining of sexual maturity in man, but the digression from the mean is slight and has no direct bearing on the original establishment of the phenomenon.

In one respect, however, the periodicity of Chusquea differs strikingly from the cycle of annuals and the aging of organisms. That the span of life of an individual Chusquea is thirty-three years is no more remarkable and is as satisfactorily explainable as is the fact that an annual lives one year, man eighty years, and a Sequoia 5,000 years. But an hypothesis which will explain these phenomena is not necessarily sufficient to account for the simultaneous flowering of fully 98 percent of the individuals of a species extending over a great stretch of country.

There is as yet, it seems to me, no adequate explanation of the behavior of Chusquea. That seasonal factors at present active bring on this simultaneous flowering is very unlikely. That past climatic influences are responsible is quite possible. But the ultimate cause I should be inclined to search for in the physical and chemical make-up of its protoplasm; fully realizing, however, the possibility, indeed the probability, that this very nature of the protoplasm has come to be what it is in part because of its past environment as well as because of its own original constitution.

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